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Global analysis of *Toxoplasma gondii* prevalence in wild avian hosts: effects of phylogeny, ecology, and detection methods

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ABSTRACT

Toxoplasma gondii is an Apicomplexan protozoan parasite that infects warm-blooded animals, including birds. Birds may play a significant role in the parasite's transmission due to their diverse habitats, diets, dispersal abilities, and potential as prey for predators. However, information on *T. gondii* infection dynamics in avian hosts is limited globally. To address this, we conducted a systematic review of 82 studies reporting *T. gondii* prevalence in wild birds. Using generalized linear mixed models, we analyzed global prevalence patterns across avian taxa and explored predictors of prevalence, including bird order, habitat type, trophic level, and lifestyle, in serological and direct (e.g., genetic and histological) detection studies. We also assessed the strength of the phylogenetic signal in *T. gondii* prevalence among avian lineages. The global distribution of studies was geographically clustered, with direct detection methods more frequently used in Europe and North America. Certain bird orders, particularly Anseriformes, Accipitriformes, and Strigiformes, exhibited higher prevalence rates, suggesting their important roles in *T. gondii* transmission. Ecological factors, such as habitat characteristics and trophic levels (e.g., omnivores), were significant predictors of infection. Although phylogenetic analysis revealed a weak phylogenetic signal, high prevalence values were observed in hawks, owls, and falcons. These findings consolidate existing knowledge and emphasize the importance of targeted surveillance efforts. They highlight critical gaps in research on *T. gondii* transmission in avian hosts and provide direction for future studies. Such insights can inform wildlife management strategies and efforts to mitigate zoonotic disease risks associated with *T. gondii*.

1. Introduction

Anthropogenic activities like deforestation, urbanization, and agricultural expansion have increased interactions between humans and wildlife, leading to an increased risk of zoonotic disease transmission (González-Barrio, 2022). Many emerging infectious diseases are zoonotic, often originating from wild animals that harbor pathogens capable of infecting humans. This "spillover" process depends on the ecological, epidemiological, and behavioral factors that determine the likelihood of human exposure to these pathogens (Plowright et al., 2017). Disease spillover poses significant risk not only for human health but to conservation, as it can lead to wildlife population declines, disrupt ecosystems, and impact conservation efforts for vulnerable and protected species (Keesing & Ostfeld, 2021; Smith et al., 2009).

One globally widespread example of a zoonotic pathogen that impacts both humans and wildlife is *Toxoplasma gondii*, a protozoan parasite responsible for the disease toxoplasmosis. The only known definitive hosts for T. gondii are felids, including domestic cats, which excrete T. gondii oocysts in their feces. These oocysts sporulate in the environment and can be acquired through consuming infected tissues or contaminated water, soil, and vegetation, creating numerous opportunities for infection in intermediate hosts (Attias et al., 2020; Dubey et al., 1998; Dubey, 2004; Dubey et al., 2013; Hill & Dubey, 2002; Al-Malki, 2021; Wilson et al., 2020). *Toxoplasma gondii* can infect a wide range of warm-blooded species but has also been found in other organisms such as bivalves (Hohweyer et al., 2013; López-Ureña et al., 2022; Shapiro et al., 2019).

Environmental transmission of T. gondii is facilitated by the parasite's ability to persist in moist soil and at mild temperatures, where it has been shown to remain viable for months to years under ideal conditions (López-Ureña et al., 2022; Marciano et al., 2020; Shapiro et al., 2019). In aquatic systems, *T. gondii* oocysts

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can be transported through runoff or wastewater to larger water systems, contaminating rivers, lakes, and coastal areas, where they have been implicated in widespread outbreaks due to the contaminated water (Dumètre & Dardé, 2003; López-Ureña et al., 2022; Marciano et al., 2020; Shapiro et al., 2019). Furthermore, bivalves in these aquatic systems, which filter large volumes of water throughout their lifetime, have been shown to accumulate *T. gondii* oocysts, creating another potential infection route into humans and wildlife (Hohweyer et al., 2013; López-Ureña et al., 2022; Shapiro et al., 2019). This environmental resilience, range of hosts, and diversity of transmission pathways complicates efforts to manage toxoplasmosis.

Toxoplasma infections affect a wide range of unsuitable and suitable intermediate hosts, including humans, domestic animals, and wildlife, often with significant health impacts. While toxoplasmosis is typically asymptomatic in healthy humans, it can cause severe complications in immunocompromised individuals and developing fetuses, including neurological damage, blindness, and toxoplasma encephalitis (Hill et al., 2005). Wildlife and domestic animals, such as sea otters and birds of prey, can experience fatal cases of toxoplasmosis, particularly when coinfected with other pathogens or exposed to high oocyst levels (Di Guardo et al., 2010; Hill et al., 2005). Additionally, behavioral changes linked to T. gondii infection have been observed in some animal species, increasing their risk of predation and thus aiding in the parasite's transmission cycle (Berdoy et al., 2000; Desmettre, 2020; Meyer et al., 2022; Poirotte et al., 2016). These wide-ranging effects highlight the need for a comprehensive approach to managing the risks associated with this resilient pathogen, including monitoring wild species and gaining an understanding of how species contribute to the infection cycle in an ecosystem.

Among wildlife, birds may represent a species group at high risk for T. gondii infection. Birds not only inhabit diverse environments, with broad diets, but also serve as potential prey for various predators, making them a potentially crucial link in the parasite's transmission (Dubey, 2002; Gerhold & Yabsley, 2007). Moreover, research indicates that migratory species may play a crucial role in spreading the parasite across ecosystems (Dini et al., 2023). However, the current understanding of T. gondii infection in naturally infected avian hosts is limited, and further research is essential to clarify the extent and impact of these infections in birds. Notably, the extent to which certain avian species are more prone to *T. gondii* infections due to their ecology, including their environments and diets, and whether certain phylogenetic lineages of birds are more susceptible to this parasite, remains to be determined. To complicate matters, different studies have used different methods to test birds for *T. gondii* infection. The main approaches are serological (detection of antibodies in blood), histological (visual detection of the parasite in host tissues), and molecular (polymerase chain reaction (PCR) to detect parasite DNA in host tissues) (Liu et al., 2019; Molaei et al., 2023). These methods have different sensitivity and thus limit transferability of results across studies (Cerqueira-Cézar et al., 2019; Liu et al., 2019).

To address this gap, and extending the scope of earlier global analyses (Chen et al., 2024; Zaki et al., 2024), our study sets out to improve our understanding of the worldwide distribution of T. gondii in avian hosts. Specifically, we aimed to (i) assess whether there is any phylogenetic signal in the occurrence of T. gondii infection among bird species and families, and (ii) identify potential ecological properties of avian species that may influence their risk of infection and why prevalence varies among different bird species. To address these, we reviewed the literature and constructed two large datasets of *T. gondii* infections in birds, a separate one for each of the two most widely used methods to detect *T. gondii*, thus accounting for methodological biases: serology and genetic testing. By focusing on the two objectives above, we provide insights into the role of birds in the transmission ecology of T. gondii and inform future efforts to monitor and mitigate infection risks across wildlife species.

2. Methods

2.1. Data compilation

A comprehensive literature search was conducted using the Web of Science and University of Otago Library databases to identify studies that tested for Toxoplasma infections in wild bird populations. The search was designed to capture studies that provide data on the prevalence, incidence, or cases of Toxoplasma among avian species in the wild. Therefore, we used the search terms "Toxoplasm* AND (bird OR avian) AND (incidence OR prevalence OR case) AND wild," yielding an initial set of 3092 articles published since 2002, when the last major review of toxoplasmosis in avian hosts was published; additionally, we included the findings/papers from that 2002 review (Dubey, 2002).

Following this broad initial search, we implemented a duplicate screening process to ensure that only unique records were considered for further inclusion (Supplementary Table S1). This step resulted in the removal of redundant records, narrowing the total number of articles to 2982. These unique articles then underwent a secondary screening phase based on predefined eligibility criteria. We aimed to include only studies that provided empirical data on the presence, prevalence, or incidence of Toxoplasma in wild birds. Because we also wanted actual numbers of birds tested and numbers found to be infected (positive) by *T. gondii*, we excluded articles that focused on domesticated or captive birds, birds that were experimentally infected, or articles that did not provide primary data on infection rates—this meant removing pooled samples and samples for which recalculating the original number of birds tested using the prevalence percentage did not yield a whole number.

A total of 82 articles met all criteria for inclusion. For each study, we recorded study location, species of birds sampled, sample sizes, diagnostic methods used to detect Toxoplasma (i.e., serology, PCR, or histopathology), and reported infection rates (i.e., proportion of infected individuals in sampled birds). Longitudinal and latitudinal coordinates were recorded for the sample's location, if given, otherwise they were obtained through Google maps using approximate location data. If no specific location was mentioned, the coordinates were set to the center of the study's country. Additionally, data on the species functional traits were obtained from the AVONET database, which includes ecological variables, morphological traits, and specific range size and geographical distribution for all bird species (Tobias et al., 2022). The functional traits analyzed include various ecological and behavioral characteristics. Habitat refers to the type of environment a species primarily inhabits (i.e. forest, grassland, or marine), while habitat density is a scaled metric from 1 to 3. A score of 1 indicates dense habitats, such as forests, dense thickets, or dense shrublands, whereas a score of 3 reflects open habitats like deserts, grasslands, rocky areas, or seashores. Migration is also scaled from 1 to 3, with 1 representing sedentary species, 2 for partially migratory species (i.e., the majority of the population undergoes a short-distance period of travel, or a small proportion of the population undertakes long-distance migration) and 3 for fully migratory species (i.e., the majority of the population migrates a long-distance) (Tobias et al., 2022). Trophic niche categorizes species based on their primary diet; categories include frugivores, granivores, nectarivores, herbivores, aquatic herbivores, invertivores, vertivores, aquatic predators, or scavengers. Lastly, primary lifestyle describes where a species spends most of its time, with classifications

including aerial (primarily in the air), terrestrial (on the ground), insessorial (perching or stationary behavior), and aquatic (in or around water) (Tobias et al., 2022). Finally, while all samples were recorded in our datasets and used for basic analyses, only species with sample sizes ≥ 25 individuals from the same study were included in complex analyses (e.g., GLMMs and phylogenetic analyses; see below for details), allowing for a more accurate representation of prevalence per bird species. Each row in the dataset represents an individual bird, either positive or negative for *T. gondii*, along with its associated ecological traits and other additional data.

The dataset (available at https://doi.org/10.6084/m9.figshare.29068073.v1) enabled us to assess the distribution and prevalence of Toxoplasma across different avian populations and species, geographical regions, as well as the influence of study methodologies. Furthermore, we determined whether specific ecological traits influence bird species infection probabilities.

2.2. Data manipulation

The datasets were imported into R (R Core Team, 2021) using the 'readxl' package (Wickham & Bryan, 2023). Following data import, summary statistics were calculated for avian orders within the dataset using the 'dplyr' package (Wickham et al., 2023). For each species in a study, we computed three key measures: total number of positive individuals (samples marked as "1″), total number of negative individuals (samples marked as "0″), and total number of records (the sum of positives and negatives). Summary statistics were checked for accuracy and then visualized using 'ggplot2′ (Wickham et al., 2024).

In what follows, our original data was split into two datasets: one for studies based on serological detection methods, and one based on studies using direct detection methods, primarily PCR and histology, hereafter referred to as direct detection. For geospatial analysis of positive *T. gondii* infections in birds, a world map was generated using the 'leaflet' package, where positive cases of *T. gondii* in individual birds are plotted according to the specified longitude and latitude coordinates (Cheng et al., 2024).

2.3. Data analyses

For both datasets—direct detection and serological detection methods—birds were grouped by order. Only orders with approximately or more than 100 bird samples for direct detection studies and 200 bird samples for serological detection studies were included. Using these datasets, a generalized linear mixed model (GLMM) was run using the 'lme4′ package, with binomial structure to account for the binary response variable (infected = 1, uninfected = 0) (Bates et al., 2024; Kuznetsova et al., 2017). For each model, the predictors were bird order, habitat, habitat density, migration, trophic niche, and primary lifestyle, with the reference level being accounted for as a random effect in the GLMM, as well as study ID (as the same study might provide data on more than one bird species). The orders with the lowest prevalence of infection (Struthioniformes for serology and Gruiformes for direct detection) were used as reference levels.

Coefficient plots with 95% confidence intervals were visualized using 'ggplot2′ (Lüdecke, 2024; Wickham et al., 2024). Finally, we calculated the Moran I value using 'spdep' and 'sf' packages to test for spatial autocorrelation, based on the latitude and longitude of sampling locations. This served to determine whether values at one location are more similar to values from nearby locations than they are to values from distant locations, and thus to confirm the statistical independence of data points (Bivand, 2024; Pebesma, 2024).

Lastly, we tested for a phylogenetic signal in *T. gondii* prevalence among various bird species. A full avian phylogenetic tree from AllBirdsHackett1.tre was loaded into R using the 'read.tre' function (Jetz et al., 2012). Using the 'keep.tip' function, trees were pruned to match the lists in the direct detection and serological datasets. Prevalence data were mapped onto the phylogenies, to enable a visualization of phylogenetic distribution of *T. gondii* prevalence among bird species. This was done using the R packages 'ape', 'tree', 'phytools', and 'dplyr', to facilitate phylogenetic tree management and data manipulation (Paradis et al., 2024; Revell, 2024; Ripley, 2023; Wickham et al., 2023). Pagel's lambda (λ) was calculated for the prevalence data to test for phylogenetic signal, using the 'phylosig' function in 'phytools' (Revell, 2024). By assigning *T. gondii* prevalence as a trait mapped across the phylogenetic tree, Pagel's lambda assesses phylogenetic influences; it has a minimum of 0 when trait values are randomly distributed among species and approaches 1 when closely related species consistently display trait values more similar than expected by chance.

3. Results

In this study, we analyzed the global occurrence of *Toxoplasma gondii* across various avian species using both direct detection and serological testing methods. Therefore, we compiled two datasets, with the one based on direct detection methods including 9980 individual birds (Supplementary Table S2) and the one based on serological detection including 19,579 individual birds (Supplementary Table S3). Our aim was to assess what functional or phylogenetic factors may play significant roles in the parasite's transmission and thus affect the prevalence of *T. gondii* infections among birds.

There was substantial variation in the total number of individuals tested, as well as in the number of positive cases, among bird families, based on both studies using serological detection methods (Fig. 1) and those using direct detection methods (Fig. 2). Generally, the families Anatidae, Accipitridae, Laridae and Columbidae have higher sample sizes as well as a higher abundance of cases, indicating that *T. gondii* is prevalent in these families. There is noticeable consistency between the datasets obtained from the two detection methods.

In contrast, the global distribution of positive cases showed slightly different patterns between serological (Fig. 3a) and direct detection methods (Fig. 3b) across continents. Serological studies were widely dispersed, appearing frequently in North America, Europe, South America, and the coast of Asia. Direct detection studies were similarly globally distributed but with greater frequency in non-coastal Asia and New Zealand. Regardless of the method used, research effort appears spatially biased, with large areas of the world lacking any reports of positive *T. gondii* infections among bird hosts.

3.1. Determinants of T. gondii prevalence

Firstly, based on direct detection methods, the GLMM results (Supplementary Table S4, Supplementary Fig. S1) indicate that among avian orders, Anseriformes generally have a significantly higher prevalence ($p = 0.045$). While other orders, such as Passeriformes and Galliformes, exhibited prevalence values that are not significantly different from the reference level (Gruiformes).

Regarding habitat types, most types demonstrated significant impacts on the response variable, with grassland ($p < 0.001$) shrubland ($p < 0.001$), human-modified habitats ($p < 0.001$), woodland ($p < 0.01$), forest ($p = 0.0112$), desert ($p = 0.0112$), and wetland ($p = 0.0141$) all being associated with on increased prevalence.

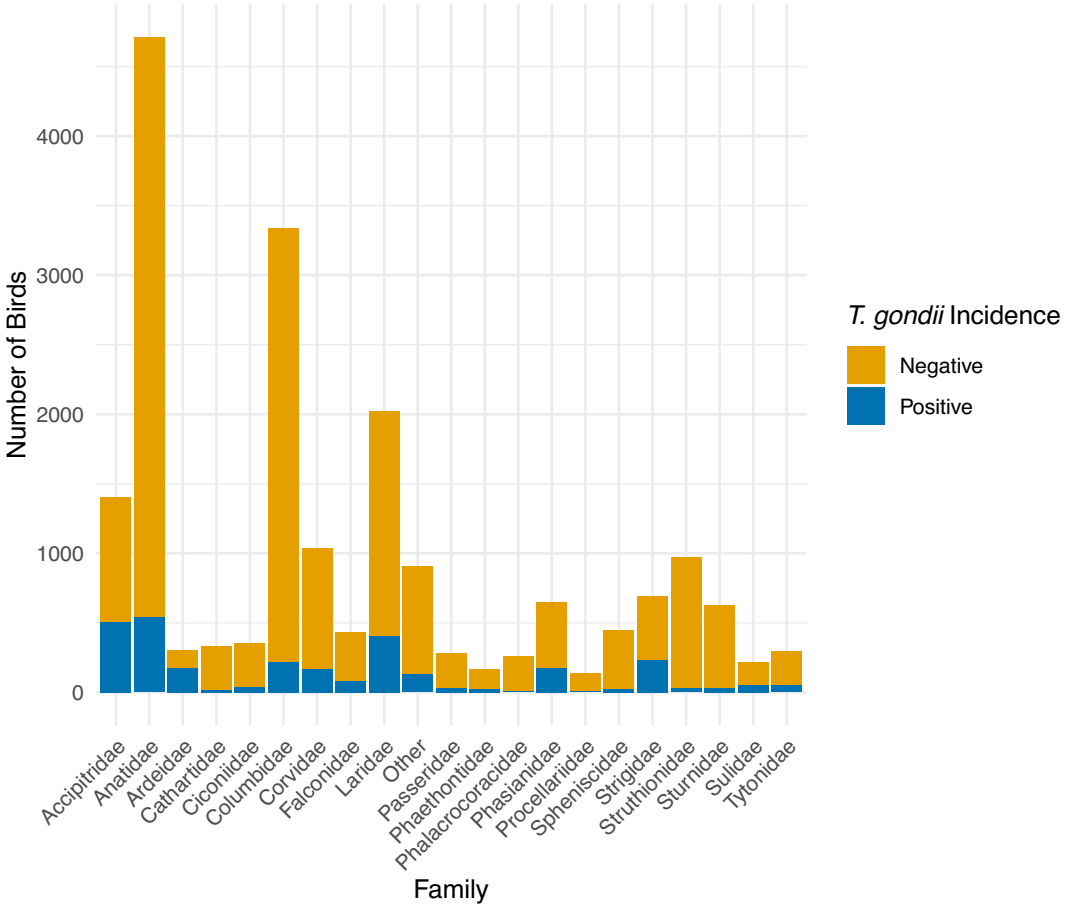

Fig. 1. Number of individual birds tested for *Toxoplasma gondii* infection, showing the top 20 famlies, shown for positive and negative cases. The remaining 49 families are combined into a 'other' category to enhance readability. Data based on studies which utilized serological detection methods.

Conversely, habitat density had a significant negative effect (estimate = –0.0458, p = 0.0011), indicating that higher habitat density is associated with an increase in prevalence.

Among trophic levels, omnivores exhibited a significantly higher prevalence (estimate = 0.0573, p = 0.0056), while scavengers had a significantly lower prevalence (estimate = –0.2417, p < 0.01). Additionally, terrestrial herbivores (p = 0.0169) and granivores (p = 0.0379) also showed significantly reduced prevalence. However, other trophic niches, including invertivores and frugivores, exhibited no significant associations with prevalence. Lastly, none of the primary lifestyle categories, including aquatic, generalists, insessorials (perching), and terrestrial species, showed a significant association with the prevalence of *T. gondii*, and neither did migration behaviors.

Secondly, based on serological detection methods, the GLMM results (Supplementary Table S5, Supplementary Fig. S2) indicate that among avian orders, Accipitriformes had the strongest positive coefficient (estimate = 0.6372, p < 0.001), indicating a strong association with *T. gondii* infections while Pelecaniformes showed the weakest positive coefficient (estimate = 0.2796, p < 0.001). Similar positive associations were observed for other orders including Strigiformes (estimate = 0.5168, p < 0.001), Passeriformes (estimate = 0.3873, p < 0.001), Columbiformes (estimate = 0.3370, p < 0.001), Falconiformes (estimate = 0.5003, p < 0.001), Galliformes (estimate = 0.2668, p < 0.001), and Ciconiiformes (estimate = 0.3970, p < 0.001).

We also found that birds whose primarily habitats are rocky surfaces tend to have higher prevalence of *T. gondii* (estimate = 0.2943, p < 0.001), indicating higher transmission in rocky environments. Additionally, birds in marine (estimate = –0.8936, p < 0.001), woodland estimate = –0.1265, p = 0.0273), and human modified (estimate = –0.1543, p < 0.01) habitats generally have lower prevalence than the reference level (Struthioniformes) suggesting lower transmission rates in these habitats. Moreover, migratory behavior showed a significant negative effect (estimate = –0.0409, p < 0.001), suggesting that migratory species may be at lower risk of *T. gondii* infections.

Regarding trophic niches, scavengers (estimate = –0.4252, p < 0.001), granivores (estimate = –0.2265, p < 0.001), omnivores (estimate = –0.1045, p = 0.004), terrestrial herbivores (estimate = –0.128, p = 0.0415), vertivores (estimate = –0.0978, p = 0.0267), and invertivores (estimate = –0.0995, p = 0.027) showed significant negative effects. Additionally, scavengers as a broad trophic level showed a positive correlation with *T. gondii* cases (estimate = 0.1861, p < 0.01). Primary lifestyle categories revealed that terrestrial birds (estimate = 0.1233, p < 0.001) showed higher prevalence, while generalist species showed a weak negative association (estimate = –0.0583, p = 0.0249). Overall, these results highlight the complex interplay between avian orders, habitats, trophic niches, and lifestyles in determining the prevalence of *T. gondii* infections.

3.2. Spatial autocorrelation

The Moran's I statistic is a measure of spatial autocorrelation, or the degree to which similar values are clustered together in space. The Moran I statistic, approximately 0.023, suggests a slight tendency for similar values to cluster together spatially. However,

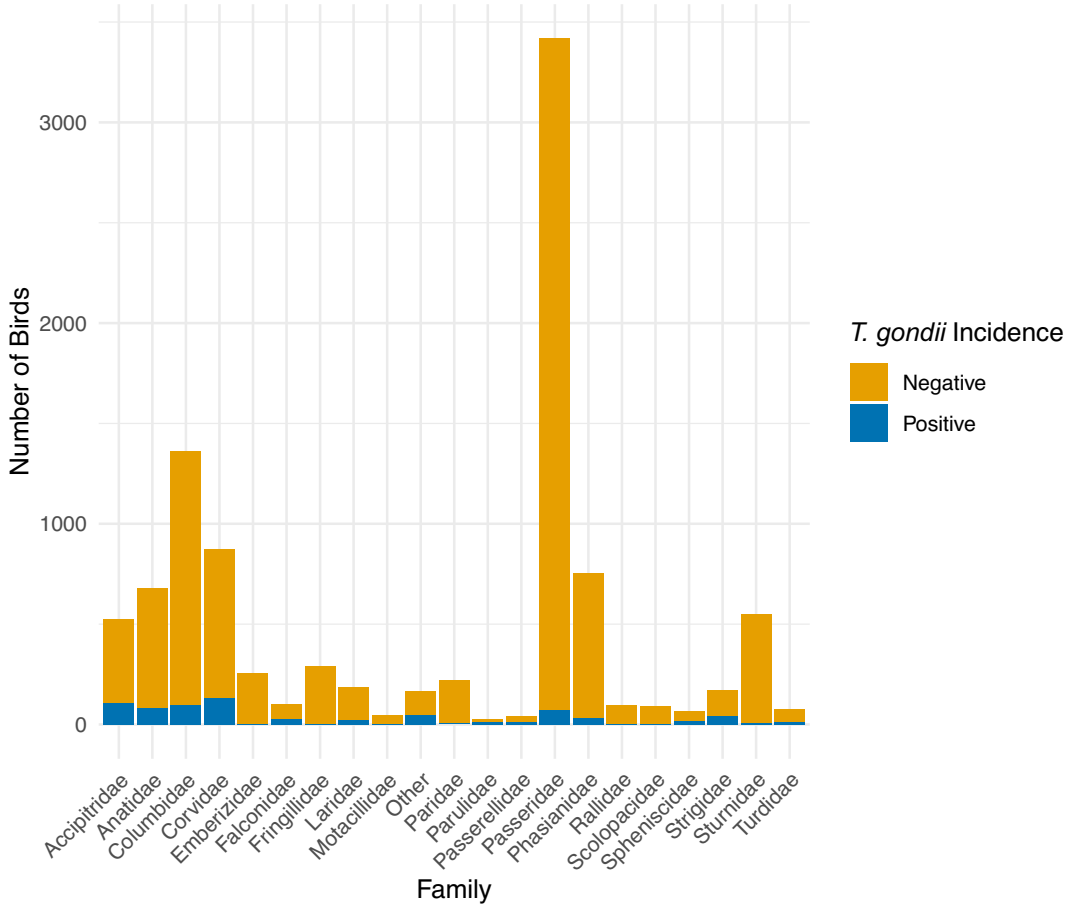

Fig. 2. Number of individual birds tested for *Toxoplasma gondii* infection, showing the top 20 famlies, shown for positive and negative cases. The remaining 42 families are combined into a 'other' category to enhance readability. Data based on studies which utilized direct detection methods (e.g., PCR and histology).

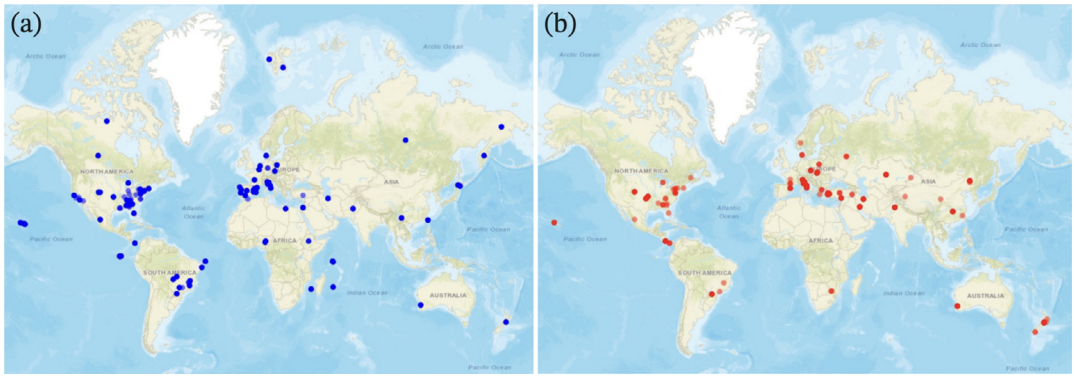

Fig. 3. A) Global distribution of serologically detected Toxoplasma gondii-positive wild bird cases, across all avian taxa. b) Global distribution of directly detected (e.g., PCR) Toxoplasma gondii-positive wild bird cases, across all avian taxa. The maps were created using the leaflet package in R (Cheng et al., 2024).

the effect is weak, given the near-zero value. The expected Moran I value under the null hypothesis of no spatial autocorrelation is close to zero (−0.00005), and the low p-value (less than 2.2×10^{-16}) provides strong evidence against the null hypothesis, confirming that the observed clustering is unlikely due to random chance.

3.3. Phylogenetic signal

The phylogenetic trees (one for data based on direct detection methods (Fig. 4a) and one for data based on serological detection methods (Fig. 4b)) visually represent the evolutionary relationships among species, while also illustrating the distribution of *T. gondii* prevalence values among bird species. The results of the phylogenetic signal analysis using Pagel's lambda for data based on direct detection methods and serological detection methods (0.1894 and 0.0929 respectively), are close to zero, indicating only weak phylogenetic structure, i.e., weak clustering of similar prevalence values among closely related lineages. Nevertheless, species within the families Falconidae (falcons), Accipitridae (hawks and kites), Strigidae (owls) and Corvidae (crows) generally tend to show high prevalence of *T. gondii*.

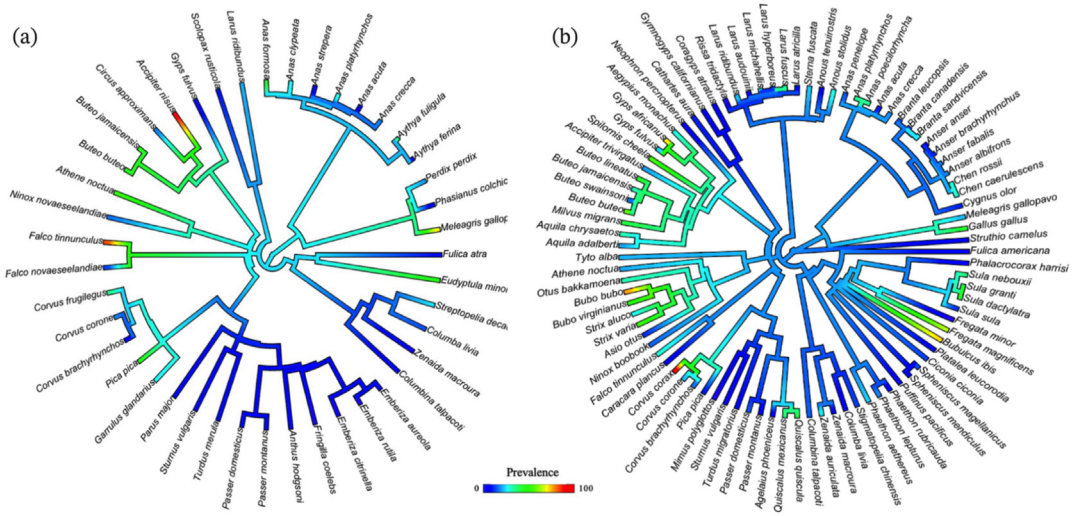

Fig. 4. Phylogenetic trees of bird species tested for *Toxoplasma gondii* infection using either (a) direct detection methods or (b) serological methods, showing the variation in prevalence of infection across the trees. Each tree includes only species for which prevalence was based on a sample size greater than 25 individuals.

4. Discussion

This study investigated variation in the prevalence of *Toxoplasma gondii* infections in wild birds, with a focus on identifying potential predictors of infection susceptibility across bird families and understanding the role that phylogeny and ecological traits play in disease transmission. Given the established importance of birds in ecosystems, especially their role as potential intermediate hosts for *T. gondii*, our findings contribute to a better understanding of the ecological dynamics of this resilient parasite in avian hosts and its broader implications for zoonotic disease risk (Dubey, 2002; Galeh et al., 2023).

The geographical distribution shows that most studies were conducted in North America and Europe, whereas very few were conducted in Africa and parts of Asia. There are also differences in the main detection method used across different regions of the world. In North America, both detection methods have been used, though serological methods appeared slightly more frequently. In Europe, studies relying on direct detection (e.g., PCR) were more common. In Africa, Asia, and Australia/New Zealand, serological methods were more commonly used, possibly due to logistical or resource constraints including limited access to direct detection technology. Overall, serological methods were more widely used globally, regardless of regional socioeconomic conditions, indicating their suitability for areas with limited laboratory infrastructure (World Health Organization, 2024). Alternatively, direct detection methods were restricted to a few regions, likely due to the resources and technical expertise required. These findings reveal regional differences in disease detection approaches: there are differences in not only the number of studies, but also the type of studies conducted in different geographic regions (Hill & Dubey, 2002). This underscores the need for more comprehensive studies in underrepresented regions to better understand the global distribution and impact of Toxoplasmosis in bird populations.

Our analysis also shows that there is variation in study effort among avian families. For instance, Accipitridae and Anatidae showed high numbers of individual birds having been tested for *T. gondii*. There may also be variability within avian families based on what detection methods were used. Importantly, we note that only one study in our dataset applied both direct detection methods and serological testing to all samples (Cerqueira-Cézar et al., 2019). A high proportion of studies used serological testing, followed by PCR only on the serologically positive samples. In the study employing both methods across all samples, certain serologically negative samples tested positive via molecular methods, and vice versa (Cerqueira-Cézar et al., 2019). This discrepancy could suggest the presence of false negatives in studies that relied on a single detection method. This also reiterates the importance of standardizing protocols so results can be directly compared between studies on a global scale.

The results of direct and serological detection analyses provide insights into the ecological and behavioral factors influencing *Toxoplasma* detection in avian species. The mixed-effects models revealed significant relationships between various predictors and the response variable. For example, terrestrial species and bird orders such as Accipitriformes, Anseriformes, and Passeriformes demonstrated strong positive associations, possibly driven by differences in social behavior, feeding ecology, or habitat use. For example, terrestrial birds may more frequently have dietary behaviors that bring them in close contact with multiple transmission pathways such as contaminated soil, water, or intermediate hosts, increasing their likelihood of ingesting the oocysts (Adeela et al., 2013; Marques et al., 2020; Schumm et al., 2023). The same applies to, birds classified as omnivorous (based on direct detection) and scavengers (based on serological detection), including species such as vultures, crows, and certain raptors, occupy trophic niches where transmission may occur through the consumption of infected prey or carcasses exposed to viable *T. gondii* cysts via contact with contaminated soil or water in the surrounding environment (Ammar et al., 2021; Wilson et al., 2024). Conversely, trophic niches such as granivores and terrestrial herbivores showed negative associations with *T. gondii* infection. These patterns underscore the importance of food web dynamics and how ecological roles influence exposure risk.

Furthermore, our findings indicate that habitat density plays a role in infection prevalence, with denser habitats (e.g., areas of dense thickets or shrubland) associated with higher prevalence, possibly due to lower species richness or reduced opportunities to encounter viable T. gondii oocysts. Additional analyses showed that when broken down by habitat types for direct detection, habitats such as grasslands, human-modified areas, and wetlands positively influenced detection probability. This may be attributed to their high biodiversity, resource availability, or anthropogenic activities that facilitate host-parasite interactions (Burgess et al., 2018; Wilson et al., 2020). Interestingly, species residing in habitats with a rocky substrate also showed higher infection

prevalence using serological detection. These environments may provide conditions conducive to oocyst persistence or harbor intermediate hosts which birds like to prey on, potentially increasing exposure risk (Wilson et al., 2024). Conversely, human-modified, marine, and woodland habitats were negatively correlated with *T. gondii* infections, suggesting that these environments may limit pathogen exposure to avian species (Lopes et al., 2021; Wilson et al., 2020). Moreover, migration was identified as a significant factor, with migratory behavior showing a slight negative association with *T. gondii* infection prevalence, possibly due to lower exposure levels while on the move.

The phylogenetic distribution of *T. gondii* prevalence across species provides some support for the ecological patterns mentioned above, such as for the influence of diet. Visually, hotspots are evident among hawks and falcons (genera *Accipiter* and *Falco*) when using direct detection methods, and among hawks, owls, and crows (genera *Bubo* and *Corvus*) when using serological testing. This pattern aligns with previous findings suggesting that diet influences *T. gondii* infections, as birds in these taxa, are primarily classified as birds of prey or scavengers, who feed on rodents, which are often infected by *T. gondii* (Mosquera et al., 2023). However, given the weak phylogenetic signals observed in the statistical tests, the patterns shown in the trees do not indicate strong evolutionary relationships.

Our analyses of the available published data indicates that *T. gondii* infections are more likely to be influenced by avian ecological traits or environmental conditions rather than inherited across related lineages. Particularly, bird species from certain avian orders (e.g., Anseriformes and Accipitriformes), living in particular habitats (e.g., rocky substrates), and within particular trophic levels, niches, or lifestyles (e.g., terrestrial omnivores) appear significantly more susceptible to infection than other birds. Conversely, birds from certain orders, such as Pelecaniformes, living in certain habitats like marine environments, etc., have lower prevalence than other birds, suggesting a complex interaction between avian ecological traits and infection risk. Additionally, these risk factors could be influenced by the local abundance and diversity of the feline definitive host.

Despite our best efforts to achieve a high-quality literature review, we acknowledge that there will be inherent bias in our dataset due to a range of factors. For instance, these include the availability of articles (e.g., articles in languages other than English and not included in Web of Science), reported data within the articles (e.g., relevant articles excluded because of inadequate data reporting), and differences among the studies themselves (i.e., data included in our dataset may be of varying quality). Our analysis relies on published data, which inevitably means varying levels of sensitivity and specificity associated with different methods of detection. Furthermore, a publication bias is likely. Studies where no *T. gondii* positive birds were found may be underrepresented in the literature, as authors may be less likely to publish. Nevertheless, we are confident that our large datasets were still representative, and that the patterns we identified are real.

The presence of *T. gondii* across diverse avian species has implications for both wildlife conservation and risk management. For conservation, understanding which bird species are most susceptible to *T. gondii*, and why, can inform habitat management and conservation strategies, especially for endangered bird populations in areas with high levels of *T. gondii* presence. In particular, terrestrial, omnivorous birds, and scavengers in contaminated habitats may require special attention to mitigate infection risk. For public health, identifying high-prevalence areas and species that interact closely with humans or domestic animals could aid in creating more targeted parasite monitoring systems. For example, enhanced surveillance of avian *T. gondii* prevalence could help predict and mitigate zoonotic risks.

Our study provides a comprehensive assessment of *T. gondii* infections in wild birds, highlighting the ecological, phylogenetic, and environmental factors that influence this parasite's transmission potential. Our findings emphasize the importance of considering ecological and evolutionary contexts when assessing disease risks in wildlife, especially for parasites with broad host ranges like *T. gondii*. By identifying avian species at higher risk of infection and the factors associated with elevated prevalence, our study contributes valuable insights for managing disease risks and conserving vulnerable bird populations.

Data accessibility

Our raw data for *T. gondii* infections in birds is available on figshare (https://doi.org/10.6084/m9.figshare.29068073.v1).

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Ethical standards

Not applicable.

CRediT authorship contribution statement

Katherine E. Buschang: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jerusha Bennett:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Clément Lagrue:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Robert Poulin:** Writing – review & editing, Supervision, Investigation, Conceptualization.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2025.06.007.

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